

INFRA-SPECIFIC DIFFERENTIATION IN THE
AMPHICARPAEA BRACTEATA (FABACEAE) SPECIES
COMPLEX: VARIETIES AND ECOTYPES

HILARY S. CALLAHAN

Department of Botany, University of Wisconsin, Madison, WI 53706

Current Address: Department of Botany, University of Tennessee,
Knoxville, TN 37996-1100

ABSTRACT. Because amphicarpy is strongly associated with heterogeneous habitats, it can be difficult to document and interpret infraspecific differentiation in amphicarpic species. In the woodland annual *Amphicarpea bracteata*, a canonical variates analysis (CVA) of morphological data from herbarium specimens provided initial support for the recognition of two distinct varieties. Subsequently, common garden and greenhouse studies were conducted with multiple populations of these two well-marked varieties, *A. bracteata* var. *comosa* and *A. bracteata* var. *bracteata*. Because the variety *comosa* is restricted to sunnier habitats while the variety *bracteata* spans a broad range of habitats, these studies included *bracteata* populations from both densely shaded and sunny habitats. CVA of the greenhouse data indicated that the varieties *comosa* and *bracteata* maintained discrete differences in leaf morphology. Thus, varietal differences are, in part, genetically based rather than solely plastic responses to the local environment. Differences between shade- and sun-native *bracteata* populations, although relatively minor, also appeared to be, in part, genetically based. Consistent with its affinity for sunnier habitats, the variety *comosa* achieved superior survivorship and fecundity under high light conditions. However, fecundity was greater in shade-native than in sun-native *bracteata* populations. In combination with trends in leaf morphology, these results support the idea that the variety *comosa* is a sun-adapted ecotype, but not the concept that shade- and sun-native *bracteata* populations are, respectively, shade- and sun-adapted.

Key Words: *Amphicarpea bracteata*, amphicarpy, canonical analysis, ecotypes, Fabaceae, infraspecific variation, phenotypic plasticity

Amphicarpic plants have dual reproductive strategies, and often one or both reproductive modes are associated with high levels of selfing and limited seed dispersal (Cheplick 1994; Cheplick and Quinn 1988). Consequently, amphicarpic species might be expected to display strong patterns of local population differentiation, reflecting genetic drift in populations with restricted gene flow, perhaps reinforced by local selection (Levin 1981, 1988). Since amphicarpy is strongly associated with spatially or temporally varying environments and phenotypic plasticity (Cheplick

and Quinn 1982; Van der Pijl 1982; Schoen and Lloyd 1984), documenting and interpreting such differentiation can be quite difficult.

Amphicarpaea bracteata (L.) Fern. exemplifies these aspects of the amphicarpic habit (Schnee and Waller 1986; Trapp 1988). In this woodland annual, production of flower and fruit morphs depends strongly on overall plant size. Accordingly, across habitats varying in light availability, there is substantial variation in whole-plant morphology and in life history traits (Schnee and Waller 1986). It remains unclear whether variation among populations represents plastic responses to local environments, genetically based differences due to past selection, genetic drift, or some combination of these processes.

Variation among populations is not the only form of infraspecific variation within *Amphicarpaea bracteata*. Turner and Fearing's (1964) taxonomic revision discusses two well-marked varieties, *A. bracteata* var. *bracteata* and *A. bracteata* var. *comosa* Fassett. The monograph illustrates the varieties' coextensive ranges, reiterating previous authors who emphasize "continuous intergradation" (Gleason and Cronquist 1963). More recent evidence, however, suggests that infraspecific taxa matching descriptions of the varieties *bracteata* and *comosa* may grow sympatrically but remain reproductively isolated (Parker 1992, 1994). Also, across a broad geographic range, multilocus enzyme electrophoresis distinguishes two varieties and possibly a third taxon that display distinct allozyme profiles and divergent leaf morphologies (Parker 1996).

Examination of herbarium sheets and observations in the field indicate that it may be fairly common to find specimens or populations corresponding to the two varieties (Fassett 1936, 1939) and possibly to Parker's (1994, 1996) descriptions of a third taxon.

The debate regarding varieties within *Amphicarpaea bracteata* has often mentioned that the varieties tend to differ in their affinities for sunny and shady habitats. For example, circumscription of *comosa* involves not only the tawny pubescence on its leaf surfaces, petioles, and stems, but also a restriction to sunnier habitats (Fassett 1936). In contrast, *bracteata* occurs across a broader range of habitats, from sunnier to very densely shaded habitats (Fassett 1936; Schnee and Waller 1986). Furthermore, there appear to be taxa with leaf morphologies that correspond to classic descriptions of either shade- or sun-adapted ecotypes: (a)

a shade-adapted, *bracteata*-like taxon with delicate, thin, broad leaflets and leaves, (b) a more sun-adapted, *bracteata*-like taxon with sparsely pubescent and much narrower leaflets and leaves (Parker 1994), and (c) the sun-adapted variety *comosa* with its dense leaf and stem pubescence and broad but sturdy, thick leaves (Figure 1; Boardman 1977; Givnish 1988).

The studies reported here are based on *a priori* recognition of these three putative taxa within the species complex. These groups are subject to careful scrutiny using multivariate data sets that quantify suites of morphological and life history traits. By comparing patterns of differentiation not only among local populations but also more broadly across the three infraspecific taxa, it may be possible to infer the extent to which these groups reflect varieties and possibly ecotypes adapted to different points along a sun-shade gradient.

To fulfill this goal, morphological differences among groups were assessed at two different spatial scales. First, across the species range, suites of leaf and floral traits were analyzed to determine whether they can consistently distinguish *comosa* from *bracteata*, and possibly a third *bracteata*-like taxon. Second, focusing locally on native populations in south-central Wisconsin, differences in leaf morphology and life history traits were assessed in controlled environments, including both a common garden and a greenhouse. Morphological analyses of native populations address an important ecological question: is variation in leaf morphology consistent with habitat affinity and expectations based on presumed functional adaptations? By incorporating not only leaf morphology but also life history traits, data sets from the common garden and greenhouse address a second ecological question: in high light conditions, are survivorship and fecundity greater in *comosa* and sun-native *bracteata* populations than in shade-native *bracteata* populations?

MATERIALS AND METHODS

Herbarium specimen survey. The 101 sheets from the North American collection at the University of Wisconsin–Madison Herbarium include collections ranging from Winnipeg, Manitoba, south to Gainesville, Florida, and from New Bedford, Massachusetts, west to the Black Hills of South Dakota. For each, varietal designations were verified and unidentified specimens

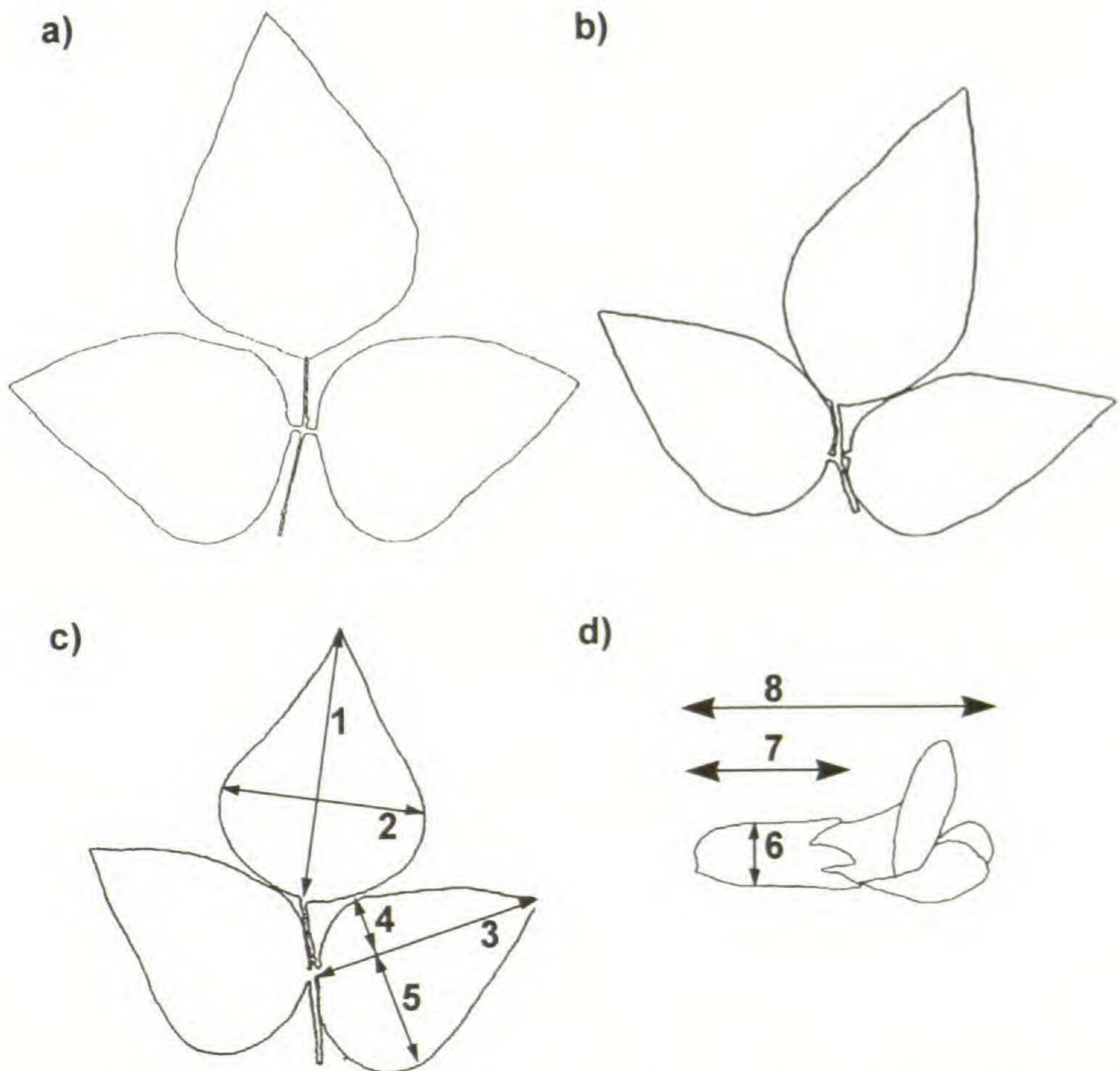


Figure 1. Leaf silhouettes of *Amphicarpaea bracteata* var. *bracteata* with (a) wide and (b) narrow terminal and lateral leaflets, coded as **w** and **n**, respectively, in herbarium specimen surveys. Parker (1991b) proposed that wider leaflets are adaptations for shade while narrower leaflets are adaptations for sun. (c) Leaf silhouette of *A. bracteata* var. *comosa*, coded as **C** in herbarium specimen surveys. Parker (1992) has suggested that despite its broad and truncate leaflets, *comosa* may be a sun specialist based on its high specific leaf area, pubescence of leaves and stems, and narrower habitat distribution. Also shown are (c) leaf and (d) floral traits measured on dried herbarium specimens: 1 = terminal leaflet length; 2 = terminal leaflet width; 3 = right lateral leaflet length; 4 = right lateral leaflet maximum width from midrib to apical edge; 5 = right lateral leaflet maximum width from midrib to basal edge; 6 = calyx width at base; 7 = calyx length; and 8 = corolla length.

were assigned to a variety (*comosa* = **C** or *bracteata* = **B**) based on density and prominence of vestiture on stems, petioles and inflorescences. In addition, all *bracteata* specimens were classified and coded as having either wide leaves and leaflets (**w**) or narrow leaves and leaflets (**n**). This scheme follows Parker

Table 1. Trait descriptions, means (standard errors), and sample sizes for leaf and floral morphology traits recorded from 101 herbarium specimens. All data were approximately normally distributed. Also reported are results of contrasts that combined categories from univariate ANOVAs. **C-B** refers to a contrast of *comosa* and *bracteata* specimens; **w-n** excludes *comosa* individuals and contrasts wide- and narrow-leaflet specimens of *bracteata*. Bonferroni-corrected significance levels are indicated. *** $p < 0.001$; ns = no significant difference.

Vegetative Traits	Trait Description				Contrasts	
	<i>comosa</i> n = 33	<i>bracteata</i> wide-leaflet n = 34	<i>bracteata</i> narrow-leaflet n = 15	C-B $F_{(1,78)}$	w-n $F_{(1,78)}$	
Petiole length (cm)	6.40 (6.00–6.80)	4.90 (4.51–5.30)	4.11 (3.51–4.69)	12.569 ***	1.255 ns	
Terminal leaflet petiolule length (mm)	1.81 (1.74–1.89)	1.34 (1.30–1.37)	1.20 (1.09–1.32)	27.794 ***	1.049 ns	
Right lateral leaflet petiolule length (mm)	0.33 (0.29–0.37)	0.33 (0.30–0.37)	0.28 (0.22–0.33)	0.279 ns	0.726 ns	
Terminal leaflet length (cm)	5.82 (5.57–6.08)	4.47 (4.22–4.72)	4.80 (4.43–5.17)	12.459 ***	0.549 ns	
Terminal leaflet maximum width (cm)	4.78 (4.52–5.04)	3.40 (3.14–3.65)	2.95 (2.57–3.34)	21.149 ***	0.912 ns	
Right lateral leaflet (RLL) length (cm)	5.41 (5.19–5.62)	4.04 (3.83–4.25)	4.00 (3.68–4.32)	23.188 ***	0.011 ns	
RLL max. width, midrib to apical edge (cm)	1.56 (1.50–1.61)	1.22 (1.16–1.27)	1.11 (1.03–1.19)	28.199 ***	1.275 ns	
RLL max. width, midrib to basal edge (cm)	2.33 (2.24–2.42)	1.66 (1.57–1.75)	1.41 (1.27–1.55)	40.929 ***	2.313 ns	

Table 1. Continued.

	Trait Description				Contrasts	
	<i>comosa</i> n = 22	<i>bracteata</i> wide-leaflet n = 26	<i>bracteata</i> narrow-leaflet n = 7		C-B	w-n
Floral traits						
Calyx width at base (nearest 0.15 mm)	16.05 (15.39–16.70)	14.39 (13.78–14.99)	14.86 (13.69–16.02)		2.344 ns	0.129 ns
Calyx length from base (nearest 0.15 mm)	37.77 (35.50–39.04)	33.62 (32.45–34.78)	33.86 (31.60–36.11)		5.048 ns	0.009 ns
Corolla length from base (nearest 0.15 mm)	75.18 (73.70–77.07)	68.92 (67.19–70.66)	73.71 (70.37–77.06)		2.101 ns	1.618 ns

(1991a, 1994), who suggested that wider leaves and leaflets may correspond to an adaptation to dense shade, while narrower leaves and leaflets may correspond to an adaptation for sunnier conditions. Parker (1992) also has suggested that, despite its broad leaflets, the pubescent and thicker stems and leaves of *comosa* may indicate adaptation to high light conditions (Figure 1).

Eight leaf morphology traits were scored from a single, fully expanded leaf, choosing the most apical leaf when there was a choice of more than one adequately preserved leaf on an herbarium sheet (Figure 1c; Table 1). Three floral traits also were scored, using the inflorescence with the greatest number of flowers and choosing the most basal aerial chasmogamous (hereafter ACH) flower that could be measured intact on the dried, pressed specimen (Figure 1d; Table 1).

For each of these 11 traits, univariate ANOVAs were conducted, after which planned contrast was used to test whether trait means differed between all *comosa* and all *bracteata* specimens. After excluding the *comosa* plants, a second planned contrast was used to test for differences between the wide-leaflet and narrow-leaflet specimens of *bracteata* (**w** vs. **n**). To adjust for possible error due to multiple comparisons, a Bonferoni procedure adjusted significance levels (to $p < 0.05/22 = 0.002$). To specify and test all hypotheses, the AMATRIX procedure of Systat 5.1 was used (Wilkinson 1990).

Next, a canonical variates analysis (CVA) also took advantage of these *a priori* groups and planned comparisons. The method optimally discriminates among groups based on linear combinations of weighted variables, or canonical variates (CVs). By examining canonical correlations (i.e., correlations between CVs and the original variables), one can interpret which traits are important for delineating groups (Pimintel 1979). To test the statistical significance of the CVA, a multivariate F-statistic was calculated and tested against an appropriate likelihood ratio criterion (here, Wilkes' λ). To facilitate visual examination of group overlap, the CVs of individual specimens were plotted, and group centroids and 50% group ellipsoids were delineated (Wilkinson 1990).

Common garden study. Sun- and shade-native populations of *bracteata* and some *comosa* plants were included in a common garden study conducted during summer 1993. Plants were collected as seedlings on May 18 at two wooded sites in Baraboo,

Wisconsin (Devil's Lake State Park and Howard I. Potter Preserve), using a stratified random array of 64 points within four 40 m² grids. At each site, two grids were located in a densely shaded area with a closed overstory canopy and another in a sunnier area with a partially open canopy (Callahan 1996). Only *bracteata* seedlings grew in both shady areas and in the sunny area at Devil's Lake. In the sunny area at the Potter Preserve, the two varieties grew sympatrically, and this protocol sampled 22 *comosa* and 42 *bracteata* individuals. Varieties were identified based on presence or absence of dense, tawny pubescence on the elongating apical meristem. Seedlings were transplanted into a random array at a common garden at the University of Wisconsin Arboretum (Lost City Forest site). The semi-open overstory canopy of this garden was similar to the sunny areas at the native sites.

Individuals were monitored for survivorship on 4 dates in 1993: June 10, June 18, June 29, and July 31. During fall 1993, I recorded production of ACH flowers and fruits by all surviving plants. In addition to an analysis of all sun-native and shade-native populations in the common garden study, I also made more detailed comparisons of the 22 *comosa* and 42 *bracteata* individuals transplanted from the sunny area at the Potter Preserve. I used χ^2 statistics to test varietal differences in two life history traits: proportions surviving to particular time points in the growing season and proportion of surviving plants that flowered.

Greenhouse study. A subsequent greenhouse study included populations of both varieties, and both sun- and shade-native populations of *bracteata*. For this study, subterranean (SCL) fruits were collected during October 1994 at both sunny and shady areas at each of five locations in the Eastern Baraboo Hills region of south-central Wisconsin, including the Potter Preserve and Devil's Lake sites. Seeds in SCL fruits are produced by cleistogamous (obligately self-fertilizing) flowers.

The sampling protocol entailed running two perpendicular 25 m transects through the populations. At 1 m intervals, I located the closest *bracteata* and *comosa* plants within 0.5 m (if any), distinguishing source plants as *comosa* or *bracteata* based on presence or absence of dense, tawny pubescence on leaves, stems, and petioles. Only *bracteata* phenotypes occurred in shady areas; both *bracteata* and *comosa* phenotypes occurred in sunny areas.

Table 2. Morphological, overall growth, and life history traits recorded in the greenhouse study (with precision of measurements indicated). Data transformations noted were used to improve normality; otherwise variables were approximately normally distributed.

Trait Abbreviation and Description	Date of Data Collection		
	3/21	4/21	6/12
Ratio of length to width for simple leaf (sl; log transformed; 0.1 cm)	x		
Number of compound leaf (cl) nodes	x	x	x
Proportion of cl nodes with axillary branches (arcsin-square root transformed)	x	x	x
Length of axillary branches from sl node (1.0 cm; log transformed)	x		x
Length of axillary branches from cl nodes (1.0 cm; log transformed)	x	x	
Terminal leaflet length and width (0.1 cm)		x	
Right lateral leaflet length and width (0.1 cm)		x	
Ratio of total dry weight of stem to leaves (1 mg; arcsin-square root transformed)			x
Ratio of number of SCL fruits to total flowers (arcsin-square root transformed)			x
Ratio of number of ACH to total aerial flowers (arcsin-square root transformed)			x

Thus, there was a total of 15 populations, 5 of each type. From each, approximately 25–30 seeds were collected and cold-stratified until the following February. Seeds were planted into standard greenhouse potting medium below a neutral 63 percent shade fabric screen to simulate light levels in sunny habitats. (Average light levels in the sunny area were approximately 30 to 35 percent of full sunlight; Callahan 1996.) Morphological and life history traits were recorded at three times: March 21, April 21, and June 12. Table 2 lists traits and precision of the measurements. With the greenhouse data set, a second CVA was performed, again taking advantage of assignments to groups specified *a priori*: the variety *comosa* (C), and sun-native (H) or shade-native (L) populations of *bracteata*.

RESULTS

The varieties *comosa* and *bracteata* differ significantly for seven of eleven traits examined, all of which are leaf morphology

traits. Between the two varieties, differences in floral traits are statistically non-significant or of only marginal significance ($0.05 < p < 0.10$). There are no statistically significant differences between the narrow-leaflet and wide-leaflet groups within *bracteata* for any of the 11 leaf or floral traits (Table 1). However, CVA supports significant separation of group centroids (Wilkes' λ test: $F = 2.695$, d.f. 22, 70, $p < 0.001$).

The first CV axis distinguishes *comosa* from *bracteata*, regardless of whether the latter is considered as two separate groups or as a single group that combines the taxa coded as **n** and **w** (Figure 2a, b). In *comosa*, lateral leaflets are broader with more truncate bases and the terminal leaflet petiolule tends to be longer (Table 3). The second CV axis, which correlates strongly with corolla length (Table 3), provides little additional separation of *comosa* from *bracteata*, but in combination with the first CV it provides moderate separation of the taxa coded as **n** and **w**. This result extends other observations of floral traits by Parker (1996) and Schively (1897), who observed differences in corolla color among *Amphicarpaea bracteata* varieties or populations. In summary, most of the specimens separate cleanly into three groups, but it is not always possible to assign individual specimens with this particular set of quantitative traits.

Different sun- and shade-native populations of *bracteata* did not differ significantly for survivorship. In contrast, focusing on transplants from the sunny area at the Potter Preserve, the two varieties differed in survivorship throughout the 1993 growing season. Of the 22 *comosa* plants at the beginning of the study, 91 percent survived until the end of the growing season. Of the 42 *bracteata* plants at the beginning of the study, about 70 percent survived until the end of June, about 50 percent survived until the end of July, and 43 percent survived until the fall when plants flowered, set fruit, and senesced. Differences in survivorship between varieties on June 27 and July 31 are statistically significant (respectively, $\chi^2 = 6.19$, $p < 0.05$; $\chi^2 = 14.05$, $p < 0.001$). Among the surviving plants, there is no significant difference between varieties in the number of plants that produced ACH flowers ($\chi^2 = 0.26$, $p > 0.50$). However, this statistical test may lack power because the sample size of surviving plants is small.

Greenhouse study. By quantifying numerous morphological and life-history traits in the greenhouse study (Table 2), signifi-

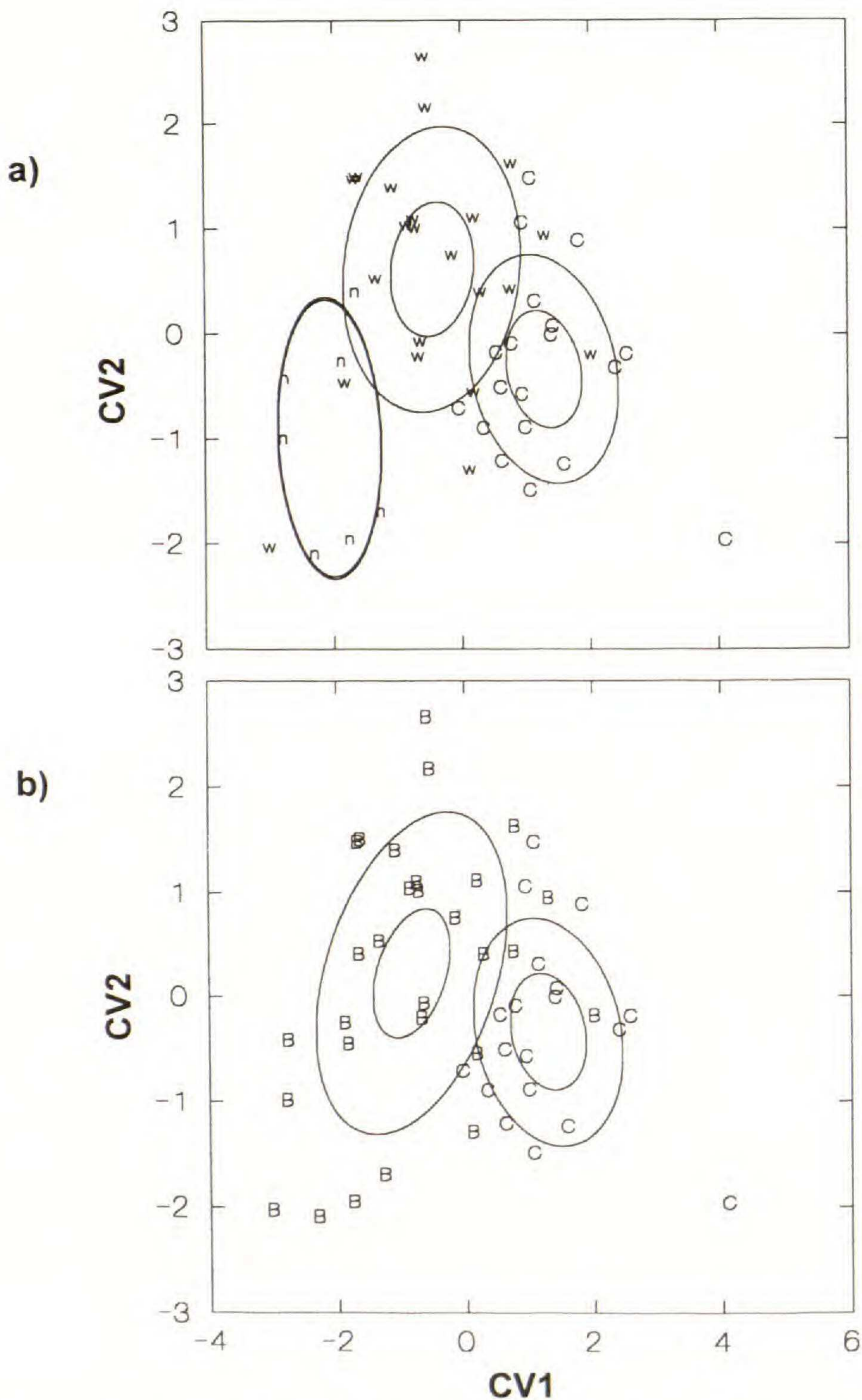


Figure 2. Plots of 95 percent group centroids and 50 percent group ellipsoids based on CVs derived from leaf and floral morphology traits measured on 101 herbarium specimens from across the species range. (a) Codes indicate *Amphicarpaea bracteata* var. *comosa* individuals (C; $n = 19$) and wide-leaflet (w; $n = 22$) and narrow-leaflet (n; $n = 7$) biotypes of *A. bracteata* var.

Table 3. Correlations between dependent variables and dependent canonical variates (CV1, CV2) from herbarium specimen survey. * Indicates three traits that correlate most strongly with each CV.

Trait	CV1	CV2
Petiole length	0.339	-0.074
Terminal leaflet petiolule length	0.592*	-0.100
Right lateral leaflet petiolule length	0.085	0.228
Terminal leaflet length	0.444	-0.433*
Terminal leaflet width	0.494	-0.174
Right lateral leaflet (RLL) length	0.558	-0.310*
RLL max. width, midrib to apical edge	0.564*	-0.081
RLL max. width, midrib to basal edge	0.642*	-0.198
Calyx width at base	0.108	-0.171
Calyx length from base	0.216	-0.273
Corolla length from base	0.157	-0.555*

cant differences were found not only between the two varieties but also between plants from sun- and shade-native *bracteata* populations. The results of CVA support separation of the group centroids (Figure 3; Wilkes' λ test, $F = 3.390$, d.f. 40, 158; $p < 0.001$).

CV1 separates *comosa* populations from sun- and shade-native *bracteata* populations quite well. More subtle differences between sun- and shade-native *bracteata* populations involve both CV1 and CV2 (Figure 3b). Generally, if plants are grown in a uniform, high light environment, terminal leaflets and lateral leaflets are longest and broadest in *comosa* plants, intermediate in *bracteata* plants from sun-native populations, and shortest and most narrow in *bracteata* plants from shade-native populations. At maturity, number of nodes, number of branches, and production of ACH flowers is greatest in *comosa* plants, intermediate in *bracteata* individuals from shade-native populations, and smallest in *bracteata* individuals drawn from sun-native populations (Table 4). Like the herbarium specimen survey, results of this greenhouse study suggest that there is some overlap among the three groups,

←

bracteata individuals described by Parker (1994). (b) The code **B** indicates *A. bracteata* var. *bracteata* regardless of whether the specimen matches descriptions of wide- or narrow-leaflet taxa.

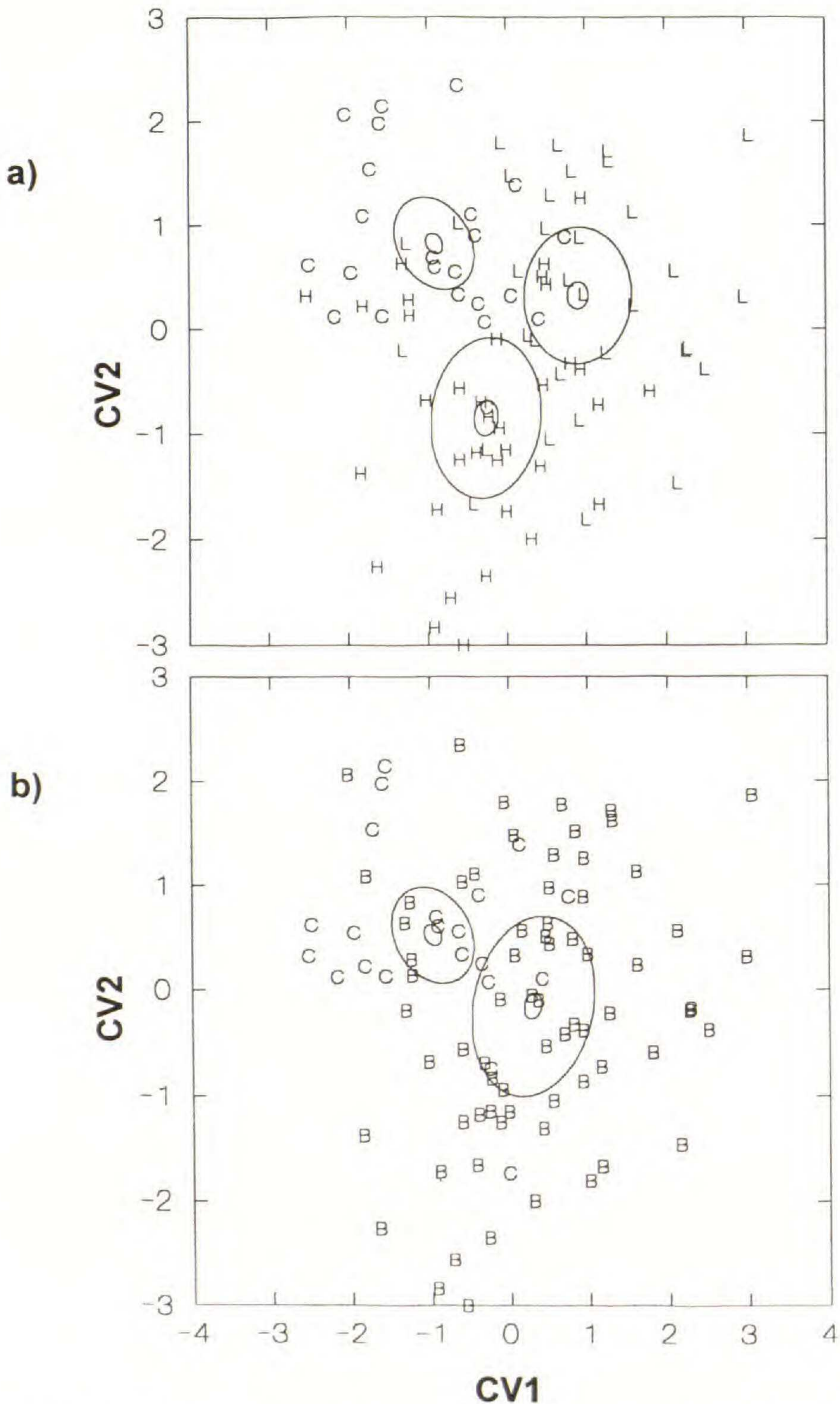


Figure 3. Plots of 95 percent group centroids and 50 percent group ellipsoids based on CVs derived from traits measured on plants cultivated in a greenhouse study. (a) Codes indicate *Amphicarpaea bracteata* var. *comosa* individuals (**C**; $n = 23$), sun-native *A. bracteata* var. *bracteata* individuals (**H**; $n = 35$), or shade-native *A. bracteata* var. *bracteata* individuals (**L**; $n =$

but the majority of individuals can be positively identified as belonging to one of the three groups.

DISCUSSION

Consistent with earlier discussions of varietal differences (Fassett 1936; Turner and Fearing 1964), no single quantitative trait can be used to identify *comosa* or *bracteata* individuals. More often than not, however, by quantifying a suite of morphological traits, one can distinguish two varieties, *comosa* and *bracteata*. A third *bracteata*-like group appears to be relatively indistinct morphologically. However, the weak evidence for divergence of **n** (narrow-leaflet) and **w** (wide-leaflet) taxa may reflect the small number of herbarium specimens that conforms to descriptions of a narrow-leaflet taxon, and associated low power of statistical tests.

Multivariate analysis of data from the greenhouse study successfully detected differentiation between sun-native and shade-native *bracteata* populations. However, morphological differences between sun- and shade-native *bracteata* populations were not concordant with the existence of distinct sun-adapted populations (with narrow leaves and leaflets) vs. shade-adapted populations (with broader leaves and leaflets). Rather, shade-native *bracteata* individuals tended to have the narrowest leaflets and leaves.

Importantly, none of the 128 *bracteata* seedlings transferred from two densely shaded areas to the sunny common garden show leaf or stem pubescence characteristic of *comosa* plants. In the high-light greenhouse environment, individuals from shade-native *bracteata* populations show no obvious pubescence. In contrast, *comosa* plants grown under dense artificial shading (95 percent of full sun) in a related study (Callahan 1996) retained this distinctive vestiture. Both locally and throughout the species' range, the presence or absence of pubescence on stems and leaf

←

33). (b) Codes indicate *A. bracteata* var. *comosa* (**C**) individuals or *A. bracteata* var. *bracteata* individuals (**B**), regardless of whether the latter are sun- or shade-native.

Table 4. Correlations between dependent variables and dependent canonical variates (CV1, CV2) from greenhouse study. * Indicates three traits that correlate most strongly with each CV.

Trait	CV1	CV2
Ratio length:width for simple leaf (sl) at first node	0.282	0.089
Early node number	-0.015	-0.111
Mid-season node number	-0.171	-0.211
Final node number	-0.084	0.284*
Early proportion branching nodes	0.236	-0.009
Mid-season proportion branching nodes	-0.298	0.000
Final proportion branching nodes	-0.061	0.284*
Early length of axillary stems from sl node	0.080	0.026
Final length of axillary stems from sl node	-0.022	0.015
Early length of branches from compound leaf (cl) nodes	-0.006	-0.004
Mid-season length of branches from cl nodes	-0.241	-0.092
Terminal leaflet length	-0.384*	0.039
Terminal leaflet width	-0.430*	-0.110
Right lateral leaflet length	-0.316	-0.032
Right lateral leaflet width	-0.330*	-0.136
Ratio of dry weight of stems:dry weight leaves	-0.233	-0.109
Ratio of number of SCL fruits:total flower number	0.261	-0.018
Ratio of number of ACH flowers:total aerial flowers	-0.288	0.432*

surfaces is perhaps the most useful trait for distinguishing two varieties.

The results of common garden work provide no support for the notion that there are distinct shade-adapted and sun-adapted ecotypes within *bracteata*, but superior survivorship of *comosa* supports the idea that *comosa* is a sun-adapted ecotype. However, survival of *comosa* seedlings in the sunny common garden environment may have been mediated by factors unrelated or only indirectly related to light levels. During summer 1993, there were unusually heavy rains and a large population of herbivores (primarily slugs) at the common garden site. Herbivores damaged plants of both varieties, but herbivore stress resulted in mortality much more frequently for *bracteata* plants than for *comosa* plants.

In the more benign greenhouse environment, survivorship was less of an issue. After the first 4 weeks of the study, all *comosa* and *bracteata* plants survived to the end of the study. However, *comosa* plants, distinguishable by leaf morphology traits, also achieved greatest vegetative growth (i.e., number of nodes and number of branches) and fecundity (number of seeds produced)

relative to *bracteata* plants, regardless of whether the latter are native to sun or shade.

In their natural habitats, shade-native *bracteata* populations typically are very small in size and produce no aerial flowers. When exposed to higher light availability in the common garden or greenhouse, these populations demonstrated the capacity to respond plastically through vigorous vegetative growth and production of numerous ACH flowers. In addition, although the greenhouse light levels contrasted sharply with light levels in their native, shady habitats, reproductive allocation in shade-native *bracteata* plants was proportionally greater than in sun-native *bracteata* plants. Thus, sun- and shade-native populations of *bracteata* do not appear to be sun- and shade-adapted, based on trends in both leaf shape and life history traits. Related work also has demonstrated that in dense artificial shade, shade-native *bracteata* plants perform poorly in comparison to both sun-native *bracteata* and *comosa* plants (Callahan 1996).

The body of evidence presented here (and previous work, Table 5) suggests that attempting to “split” *Amphicarpaea bracteata* into three distinct infraspecific taxa may be unwarranted. However, the tendency to “lump” or de-emphasize two well-marked and historically recognized varieties within *A. bracteata* probably should be reversed, especially because the two varieties seem to have distinct ecological tolerances (i.e., *comosa* is a sun specialist, while *bracteata* can tolerate environments ranging from quite sunny to very densely shaded). In addition, the varieties *comosa* and *bracteata* distinguished in these morphological and ecological studies are concordant with groups differentiated by multilocus enzyme electrophoresis and by compatibility with strains of symbiotic nodule-forming bacteria (Parker 1996). Although open-pollinated ACH flowers often produce fruits in the field, natural hybridization between the two varieties is probably quite rare in nature, since even hand-pollination seldom produces mature fruits (Wilkinson, pers. comm; pers. obs.), and on average hybrid progeny have reduced vigor (Parker 1992).

It may be taxonomically more convenient to recognize only a single species, but recognizing two varieties within *Amphicarpaea bracteata* may make it possible to use a comparative approach to better understand the evolutionary ecology of *Amphicarpaea*'s rhizobial mutualisms (Parker 1995; Spoerke et al. 1996; Wilkinson et al. 1996), host-specific pathogens (Levin

Table 5. Summary of evidence supporting the recognition of distinct infraspecific taxa within the *Amphicarphaea bracteata* species complex. References: ^A Fassett 1939; ^B Turner and Fearing 1964; ^C Parker 1992; ^D Parker 1994; ^E Parker 1996; ^F this publication.

Type of Evidence	<i>comosa</i> from <i>bracteata</i>	Taxa Distinguished	Within <i>bracteata</i>
Habitat distribution	<i>comosa</i> restricted to sunnier sites; <i>bracteata</i> more widespread; geographic ranges coextensive ^{A, B, C, E, F}	Taxa within <i>bracteata</i> may be differentiated although not necessarily adapted for sun or shade habitats ^{C, D, E, F}	
Vegetative morphology	<i>comosa</i> has dense, tawny hairs and stouter stems; <i>bracteata</i> is smoother and more slender ^{A, E, F}	Populations native to low light have narrower terminal leaflets and more rounded, narrower lateral leaflet bases ^E	
Floral morphology	<i>comosa</i> has flowers with more intense purple pigmentation; <i>bracteata</i> has paler to nearly white flowers ^{C, G} ; <i>comosa</i> has shorter corollas ^F	Longer corolla length within <i>bracteata</i> ^F	
Artificial crosses between taxa	Artificial crosses between <i>comosa</i> and <i>bracteata</i> are possible but difficult; F3 progeny show reduced mean fitness ^C	Not investigated	
Multilocus enzyme electrophoresis	A distinct <i>bracteata</i> -like lineage exists, showing no overlap with <i>comosa</i> , very few heterozygotes and no evidence for hybridization, despite local sympatry ^E	Two lineages can be distinguished, one closely resembling <i>bracteata</i> plants, the other showing some affinities to the variety <i>comosa</i> ^E	

1988; Parker 1991b), or complex and phenotypically plastic reproductive habits (Callahan 1996) within this common but unusual native species.

ACKNOWLEDGMENTS. This work was completed in partial fulfillment of the requirements for the Ph.D., supervised by D. M. Waller. I thank H. Ballard for discussions about scoring and analysis and for comments on the manuscript, which also benefited from comments by anonymous reviewers. R. Phyllky, B. Lynch, and K. Herschbel assisted in the garden or greenhouse. I gratefully acknowledge the University of Wisconsin–Madison Herbarium and its staff. Generous financial assistance came from the UW-Madison's J. J. Davis Fund and the Lois Almon Small Grants Program of the Wisconsin Academy of Sciences, Arts, and Letters, the Wisconsin Department of Natural Resources-Bureau of Endangered Resources and the Wisconsin Nature Conservancy.

LITERATURE CITED

- BOARDMAN, N. K. 1977. Comparative photosynthesis of sun and shade plants. *Annual Rev. Pl. Physiol.* 28: 355–377.
- CALLAHAN, H. C. 1996. Phenotypic plasticity in response to light availability: comparisons of varieties, ecotypes, and habitats. Ph.D. dissertation, University of Wisconsin, Madison, WI.
- CHEPLICK, G. P. 1994. Life history evolution in amphicarpic plants. *Pl. Spec. Biol.* 9: 119–131.
- AND J. A. QUINN. 1982. *Amphicarpum purshii* and the “pessimistic strategy” in amphicarpic annuals with subterranean fruit. *Oecologia* 52: 327–332.
- AND ———. 1988. Quantitative genetic variation of life history traits in amphicarpic peanutgrass (*Amphicarpum purshii*) and its evolutionary significance. *Amer. J. Bot.* 75: 123–131.
- FASSETT, N. C. 1936. Notes from the herbarium of the University of Wisconsin XIII. *Rhodora* 38: 95.
- . 1939. The leguminous plants of Wisconsin. University of Wisconsin Press, Madison, WI.
- GIVNISH, T. J. 1988. Adaptation to Sun and Shade: a Whole Plant Perspective, pp. 64–92. *In*: J. R. Evans, S. von Caemmerer and W. W. Adams, eds., *Ecology of Photosynthesis in Sun and Shade*. CSIRO, Melbourne.
- GLEASON, H. A. AND A. CRONQUIST. 1963. *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*. Van Nostrand Reinhold Company, New York.
- LEVIN, D. A. 1981. Dispersal versus gene flow in plants. *Ann. Missouri Bot. Gard.* 68: 232–253.
- . 1988. Local Differentiation and the Breeding Structure of Plant

- Populations, pp. 305–329. *In*: L. D. Gottlieb and S. K. Jain, eds., *Plant Evolutionary Biology*. Chapman and Hall, New York.
- PARKER, M. A. 1991a. Local genetic differentiation for disease resistance in a selfing annual. *Biol. J. Linn. Soc.* 42: 337–349.
- . 1991b. Nonadaptive evolution of disease resistance in an annual legume. *Evolution* 45: 1209–1217.
- . 1992. Outbreeding depression in a selfing annual. *Evolution* 46: 837–841.
- . 1994. Evolution in natural and experimental populations of *Amphicarpaea bracteata*. *J. Evol. Biol.* 7: 567–579.
- . 1995. Plant fitness variation caused by different mutualist genotypes. *Ecology* 76: 1525–1535.
- . 1996. Cryptic species within *Amphicarpaea bracteata* (Leguminosae): Evidence from isozymes, morphology, and pathogen specificity. *Canad. J. Bot.* 74: 1640–1650.
- PIMINTEL, D. 1979. *Morphometrics: the Multivariate Analysis of Biological Data*. Kendall/Hunt Publishing, Dubuque, IA.
- SCHIVELY, A. 1897. Contributions to the life history of *Amphicarpaea monoica*. *Contrib. U. Penn. Bot. Lab.* 1: 270–363.
- SCHNEE, B. K. AND D. M. WALLER. 1986. Reproductive behavior of *Amphicarpaea bracteata* (Leguminosae), an amphicarpic annual. *Amer. J. Bot.* 73: 376–386.
- SCHOEN, D. J. AND D. G. LLOYD. 1984. The selection of cleistogamy and heteromorphic diaspores. *Biol. J. Linn. Soc.* 23: 303–322.
- SPOERKE, J. M., H. H. WILKINSON, AND M. A. PARKER. 1996. Nonrandom genotypic associations in a legume—*Bradyrhizobium* mutualism. *Evolution* 50: 146–154.
- TRAPP, E. J. 1988. Dispersal of heteromorphic seeds in *Amphicarpaea bracteata* (Fabaceae). *Amer. J. Bot.* 75: 1535–1539.
- TURNER, B. L. AND O. S. FEARING. 1964. A taxonomic study of the genus *Amphicarpaea*. *Southw. Naturalist* 9: 297–218.
- VAN DER PIJL, L. 1982. *Principles of Dispersal in Higher Plants*, 3rd ed. Springer-Verlag, Berlin.
- WILKINSON, H. H., J. M. SPOERKE, AND M. A. PARKER. 1996. Divergence in symbiotic compatibility in a legume-*Bradyrhizobium* mutualism. *Evolution* 50: 1470–1477.
- WILKINSON, L. 1990. *Systat*. Systat, Inc., Evanston, IL.